

THE SYSTEMATIC RELATIONSHIP OF  
*ASARINA PROCUMBENS* TO NEW WORLD SPECIES IN  
TRIBE ANTIRRHINEAE (SCROPHULARIACEAE)

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ABSTRACT

A broad-based examination of *Asarina* s. str. has been undertaken to elucidate its systematic and phylogeographic relationship to New World species in tribe Antirrhineae. *Asarina procumbens* is differentiated from Old World and New World species by a combination of distinctive characters: procumbent stems, opposite leaves, orbiculate to reniform laminas, solitary flowers in leaf axils, large personate corollas, and globose capsules. Although the pollen morphology and seed coat anatomy of *Asarina* s. str. are shared with some taxa in the New World, *A. procumbens* is cross-incompatible with purported congeneric species and differs from native American species by three unique features: opposite leaves with orbiculate to cordiform laminas, a chromosome base number of nine, and a bullate-corrugate seed coat ornamentation. It is hypothesized that *A. procumbens* is more closely related to Old World species, that *Asarina* sensu Pennell delimits an unnatural and heterogeneous assemblage of species, and that *Asarina*, unlike *Antirrhinum*, does not represent a genus with a North American—European Mediterranean disjunction.

*Asarina procumbens* Mill. is an herbaceous perennial in tribe Antirrhineae confined to calcareous habitats from 300 to 800 m in the Pyrenees Mountains of southern France and northeastern Spain. This species has been recognized in most twentieth century treatments of the Scrophulariaceae (Rothmaler 1943; but not in Melchior 1964) and the European flora (Hartl 1965, Webb 1972) as the sole species constituting the genus *Asarina* Mill. Although many authors (Bentham 1846, Wettstein 1891, Rothmaler 1943) have recognized *Asarina* s. str. as a monotypic taxon, its ranking at the level of genus has not been uniform. *Asarina* has been either accorded generic rank (e.g., Quer y Martinez 1762, Moench 1802) or recognized as a subgenus (Reichenbach 1828, Rouy 1909) or section (Chavannes 1833, Bentham 1846, 1876, Wettstein 1891) in *Antirrhinum* L. *Asarina procumbens* has been segregated from Old World species in *Antirrhinum* and from species in New World *Antirrhinum* sect. *Saerorhinum* A. Gray (sensu Rothmaler 1956) on the basis of several distinctive vegetative, floral, and fruit characters (Rothmaler 1943).

Contrary to most supraspecific concepts in the tribe, *Asarina*'s taxonomic boundaries were greatly expanded when Pennell (1947) transferred 15 North American species into it and did not delineate

any infrageneric groups. The species included in Pennell's amplified genus had previously been treated in several supraspecific taxa by other authors. For example, Bentham (1876) and Wettstein (1891) had recognized the species in *Asarina* sensu Pennell in five sections in two genera (*Antirrhinum* sects. *Asarina* and *Maurandella* A. Gray; *Maurandya* Ort. sects. *Eumaurandya* (A. Gray) I. M. Johnston., *Epixiphium* (Engelm. ex A. Gray) A. Gray, and *Lophospermum* (D. Don) A. Gray); Rothmaler (1943) had placed the taxa in six genera (*Asarina*, *Neogaerrhinum* Rothm., *Maurandella* (A. Gray) Rothm., *Maurandya*, *Epixiphium* (Engelm. ex A. Gray) Munz, and *Lophospermum* D. Don).

The rationale behind Pennell's mass transfer was "the form of the foliage and also the large flaring corollas . . ." (Pennell 1947, p. 174) supposedly shared by *A. procumbens* and some native American taxa. The floral diversity encompassed in Pennell's expanded *Asarina* was dismissed as adaptation to specific pollinators; polymorphism among other key characters (e.g., capsule shape, seed ornamentation, phyllotaxy, lamina outline and venation, stem type) was not addressed. Although certain authors regarded Pennell's (1947) expanded *Asarina* as unnatural (Johnston 1950, Munz 1959), *Asarina* sensu Pennell has been followed in some recent taxonomic, floristic, and horticultural treatments (DeWolf 1956, Shreve and Wiggins 1968, St. John 1973, Bailey and Bailey 1976, Wiggins 1980).

In order to assess critically the taxonomic and phylogenetic relationships of *Asarina* s. str., an examination of *A. procumbens* has been undertaken that incorporates morphological, geographical, anatomical, chromosomal, palynological, and crossability data. The present study represents the first report of seed coat microsculpturing and anatomical pattern, pollen morphology, and artificial hybridization with New World species for *A. procumbens*. It also presents the first published chromosome count for a species in *Neogaerrhinum*. The primary aims of the investigation have been to gather new systematic information on *A. procumbens*, assess the data to elucidate the tribal affinities of *Asarina* s. str., and evaluate Pennell's (1947) expanded generic concept of *Asarina*. The nomenclature used in the text has followed Rothmaler (1943) or Elisens (1985a).

#### MATERIALS AND METHODS

Comparative macromorphological studies of *Asarina procumbens* have been based on examination of herbarium specimens from F, MO, NY, PH, TEX-LL, and US as well as material cultivated from seed supplied by the Barcelona, Dijon, and Leipzig botanical gardens. Voucher specimens for all descriptive and experimental studies are on deposit at the University of Texas Herbarium (TEX); collection data are listed in the Appendix.

Mature seeds for morphological and anatomical studies were based on samples supplied by botanical gardens. Each sample was 1) prepared for and examined with scanning electron microscopy (SEM) and 2) paraffin-embedded, stained, sectioned, and observed using light microscopy. Preparative procedures and materials were similar to those reported in Elisens and Tomb (1983) and Elisens (1985b).

Bud material for meiotic chromosome counts was obtained from glasshouse-grown individuals propagated from seed supplied by botanical gardens (*A. procumbens*) or the author's field collections (*Neogaerrhinum*). Buds were fixed in freshly mixed chloroform, absolute ethanol, and glacial acetic acid (4:3:1, v/v/v). Root-tips for mitotic counts were obtained from germinating seeds treated in a saturated 8-hydroxyquinoline solution. Chromosomes were stained with aceto-orcein.

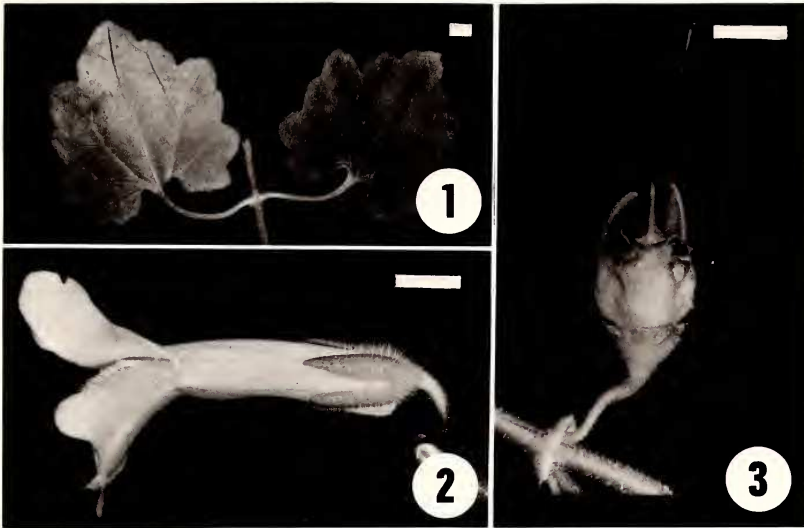
Pollen grains, obtained from fresh anthers, were dehydrated in acetic acid, acetolysed, and prepared using procedures and materials outlined in Elisens (1985a). The glycerin jelly-mounted grains were measured using light microscopy and observed and photographed using the SEM facilities at the Kansas Agricultural Experiment Station. Terminology for the exo- and endomorphology is that of Moore and Webb (1978).

Investigations of reproductive biology were conducted on plants from 13 populations representing 12 species in *Asarina* sensu Pennell that were grown from field-collected seed (North American taxa) or seed supplied by botanical gardens (*Asarina procumbens*) in the glasshouse facilities at the University of Texas and Miami University. Crossability and compatibility studies were undertaken on emasculated flowers with hand pollinations performed with fresh pollen using forceps dipped in 95% ethanol after each pollen transfer. Artificial pollinations that resulted in capsule development and seed set were considered successful crosses. Estimates of pollen fertilities were determined using cotton blue in lactophenol; 300 grains were scored for each flower and 2–3 flowers were examined per individual.

## RESULTS

Within tribe Antirrhineae, *Asarina* s. str. is distinctive because of its procumbent stems, opposite leaves, orbiculate to cordiform, glandular-pubescent laminae and palmate venation (Fig. 1); solitary, axillary flowers; lanceolate, apically-distinct calyx segments and large personate corollas (Fig. 2); and globose symmetric capsules (Fig. 3). No other taxon in the Antirrhineae has this combination of macro-morphological characters. An opposite leaf arrangement with orbiculate to cordiform laminae is not found among any New World taxon.

The bullate-corrugate seed coat ornamentation pattern (Fig. 4) of

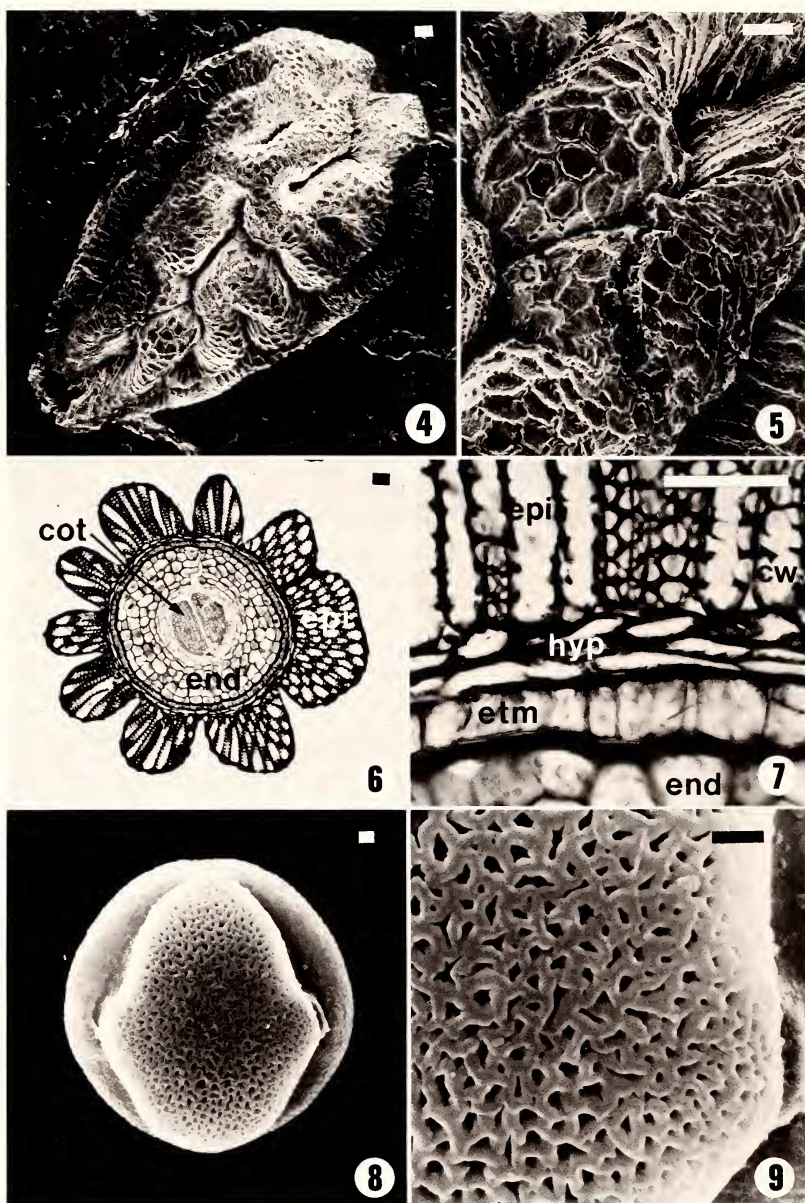


FIGS. 1-3. Photographs of distinctive morphological features of *Asarina procumbens*, Elisens 799. Scale lines equal 5.0 mm. FIG. 1. Leaf attachment, outline, and vestiture; left leaf abaxial surface, right leaf adaxial surface. FIG. 2. Calyx and corolla. FIG. 3. Mature capsule; three calyx segments removed.

*A. procumbens* is different from the seed morphology of any New World species in the tribe. The expanded crests on the seed surface form a characteristic reticulated pattern and are covered with interconnected ridges of low relief made up of radial cell walls (Fig. 5). The outer epidermal cell walls lack any protuberances (Fig. 5) similar to those found on expanded crests and tubercles in *Maurandya* and *Lophospermum* (Elisens and Tomb 1983). Mean seed lengths within *A. procumbens* are 1.52 mm long (SD = 0.16 mm,  $n = 60$ ); the seeds weigh an average 0.20 mg ( $n = 100$ ). The seed coat anatomical pattern of *A. procumbens* is an epidermis with 90% to 95% of the cells radially elongate (Fig. 6) and a hypodermis of one to three flattened layers (Fig. 7). Reticulated thickenings are present in the epidermal cells (Figs. 6, 7) and are responsible for the ribbed appearance of the radial cell walls visible on the seed surface (Fig. 5). The differentially elongated epidermal cells are solely responsible for the exotestal relief (previously noted by Bachmann 1880).

The pollen morphology of *A. procumbens* was examined from one collection. The grains are subspheroidal, trizonocolporate (Fig. 8), and have a perforate-tectate exine pattern (Fig. 9) with the perforations less than 1  $\mu$ m in diameter. The mean equatorial diameter





FIGS. 4-9. Photomicrographs of seed and pollen of *Asarina procumbens*. Key to labeling: cot, cotyledon; cw, cell wall; emb, embryo; end, endosperm; epi, epidermis; etm, endothelium; hyp, hypodermis. FIGS. 4-5. Scanning electron micrographs, seed; *Elisens* 613. Scale lines equal 0.05 mm. FIGS. 6-7. Light micrographs, transversely-sectioned seed; *Elisens* 613. Scale lines equal 0.05 mm. FIGS. 8-9. Scanning electron micrographs, pollen; *Elisens* 799. Scale lines equal 1  $\mu$ m.

of the pollen is  $19.81\ \mu\text{m}$  with a polar diameter/equatorial diameter (P/E) ratio of 1.13.

The chromosome base number of *A. procumbens* is  $x = 9$ . Meiotic chromosome number determinations for *A. procumbens* were obtained from two collections. These counts, as well as Jackson's (1971) unpublished ones from four European botanical garden seed samples, verify the  $2n = 18$  reported by Heitz (1927). A mitotic count of  $2n = 30$  was also obtained for one population of *Neogaerrhinum filipes* (see Appendix).

Crossability studies have been undertaken between *A. procumbens* and 11 American species in *Asarina* sensu Pennell. Even though pollen fertilities (93%–98%) were uniformly high for all plants, the twenty directional crosses attempted (162 hand pollinations) resulted in no capsule or seed set. In all instances, gynoecea from emasculated flowers of *A. procumbens* aborted within two weeks after anthesis whether they received no pollen or pollen from the other species. Reciprocal crosses also resulted in ovary abortion. Untreated flowers had successful capsule and seed set (25/25) indicating that *A. procumbens* is self-compatible and autogamous. Because unpollinated emasculated flowers or those pollinated from different species did not set capsules, *A. procumbens* exhibited no evidence of apomixis. Purported congeners in Pennell's (1947) expanded *Asarina* are uniformly self-compatible, autogamous (except for *Mabrya geniculata* (Rob. & Fernald) Elisens), and also showed no evidence of apomixis (Elisens 1985a).

## DISCUSSION

The systematic information reported in this study supports the taxonomic segregation of *Asarina* s. str. from Old World and New World genera in tribe Antirrhineae. Among the New World taxa, *A. procumbens* can be readily distinguished from each native genus by a combination of distinctive characters. Additionally, *A. procumbens* has several unique characters not found in any native American species: an opposite phyllotaxy with orbiculate to reniform laminas, a bullate-corrugate seed surface sculpturing pattern, and a chromosome base number of nine. The pollen morphology and testal anatomy are shared with some New World taxa.

Among seeds of New World taxa, the bullate-corrugate exotestal ornamentation pattern is most similar to the tumid tuberculate/cristate pattern found on seeds in *Maurandya* subg. *Maurandya* and some *Mabrya* Elisens species (Elisens and Tomb 1983, Elisens 1985a). The seed surfaces of the last two taxa have minute protuberances on the outer tangential and radial epidermal cell walls; similar protuberances are lacking on the seeds of *A. procumbens*. Mean seed lengths and weights are in the range of the nonalate seeds of *Mau-*

*randya* and *Mabrya* (Elisens and Tomb 1983). The seed coat anatomical pattern of *A. procumbens* is similar to testae of *Maurandya* subg. *Maurandya*, *Mabrya*, and *Holmgrenanthe* Elisens (Elisens 1985b). The testal anatomy of very few Old World species has been examined (Bachmann 1880). Both the seed coat morphological and anatomical pattern of *Antirrhinum* sect. *Saerorhinum*, *Neogaerrhinum*, *Pseudorontium* (A. Gray) Rothm., *Gambelia* Nutt., and other *Antirrhinum* segregates in the New World are different from *Asarina procumbens* (Elisens and Tomb 1983, Elisens 1985b).

The pollen exine pattern of *A. procumbens* is found also in *Maurandya*, *Mabrya*, *Lophospermum* (Elisens 1985a), *Neogaerrhinum*, *Galvezia* Dombey ex Juss., and some Old World and New World *Antirrhinum* species (Elisens, unpubl. data). Similar mean equatorial pollen diameters to *A. procumbens* are found among New World species (15.74 to 25.54  $\mu\text{m}$ ). The pollen P/E ratio of *A. procumbens* (1.13) is slightly outside the range of the American species (0.96 to 1.10) except for *Linaria texana* Scheele which has a P/E of 1.34 and some Old World species in *Antirrhinum* and *Chaenarrhinum* Reichb. (Elisens, unpubl. data). Because the pollen exine pattern, dimensions, and shape of *A. procumbens* are widespread in the Antirrhineae, pollen morphology appears to be of limited utility in elucidating the taxonomic or phylogenetic relationships of *Asarina* s. str.

No New World species in tribe Antirrhineae has a base chromosome number of nine, although *Anarrhinum* Desf. and *Kickxia* Dumort. are Old World genera with  $x = 9$ . Other Old World base numbers are  $x = 8$ , 7, and 6 (Fedorov 1969). New World tribal base numbers are 15 (*Galvezia*, *Mohavea* A. Gray, some *Antirrhinum* species, *Neogaerrhinum*), 13 (*Pseudorontium*), 12 (*Maurandya*, *Mabrya*, *Lophospermum*), 8 (*Antirrhinum*), and 6 (*Linaria* Mill.) (Günther and Rothmaler 1963, Raven et al. 1965, Jackson and Spellenberg 1973). The New World and Old World base numbers suggest that aneuploidy has been important in trans-specific evolution in the Antirrhineae (Elisens 1985a). If this is the case, the base number of nine for *Asarina* s. str. is clearly anomalous in the New World.

The Old World distribution of *A. procumbens* does not preclude automatically the segregation of *Asarina* s. str. from New World genera. Within the Antirrhineae, *Antirrhinum* and *Linaria* have Old World and New World species, although New World species in these genera usually are placed in different sections. Several North American species in *Antirrhinum* occur in habitats similar to *A. procumbens*; *Antirrhinum* also has a North American-European Mediterranean disjunct pattern (Rothmaler 1956, Raven 1973). The marked morphological and chromosomal differentiation of *A. procumbens* from New World Antirrhineae suggest, however, that *Asarina* s. str. is phylogenetically distant from New World species in *Antirrhinum* and other native American taxa.



The complete cross-incompatibility of *Asarina procumbens* with eleven species from *Neogaerrhinum* (= *Antirrhinum* sect. *Maurandella* p.p.), *Maurandya*, *Mabrya*, and *Lophospermum* further reinforces the view that *Asarina* s. str. is evolutionarily very distant from New World genera in the Antirrhineae. Species from these four genera were transferred into *Asarina* by Pennell (1947). As noted by Grant (1981), the general interspecific crossability pattern in the Scrophulariaceae (and many perennial herbs with prominent species-to-species differences in floral mechanism) is for congeneric species to be interfertile within wide limits (e.g., Garber and Gorsic 1956, Yeo 1966, Vickery 1978). This pattern occurs within the Antirrhineae in *Antirrhinum* (Baur 1932, Mather 1947), *Linaria* (Viano 1978), and subtribe Maurandyinae (Elisens 1982). Baur (1914, 1932) has previously demonstrated that *Asarina procumbens* is cross-incompatible with several Old World *Antirrhinum* species as well.

*Asarina* sensu Pennell (1947) is extremely polymorphic and incorporates three chromosome base numbers (15, 12, 9), suggesting that Pennell's expanded genus is an unnatural assemblage of species. The heterogeneity within the amplified *Asarina* is in distinct contrast to the variation pattern characteristic of most generic concepts in the tribe (e.g., Wettstein 1891, Rothmaler 1943, Elisens 1985a, D. Sutton, unpubl. data). Other than solitary flowers in the leaf axils (found in other taxa in the tribe), most potentially unifying characters in *Asarina* sensu Pennell (1947) are those generally used to characterize the tribe or family. Not even *Linaria* or *Antirrhinum*, the largest genera in the Antirrhineae, encompass the morphological diversity of stem, leaf, floral, and fruit characters found in *Asarina* s. lat. Pennell based his expanded genus concept on very few morphological characters: stem type, lamina outline, corolla type, and, to a lesser extent, capsule shape; none of these "key" characters is monomorphic within his boundaries of *Asarina*. The expanded genus can be divided into several chromosomally- and morphologically-coherent segregate taxa, such as the four genera constituting subtribe Maurandyinae (Elisens 1985a) and the genus *Neogaerrhinum* (Rothmaler 1943).

In summary, the findings of the present study indicate that *Asarina procumbens* is morphologically, chromosomally, and geographically different from its purported New World congeners or any New World Antirrhineae species. Furthermore, it is recommended that neither the generic concept of Pennell (1947) nor the purported North American—European Mediterranean disjunction in *Asarina* be recognized. Considering its chromosome base number, shared by other Old World Antirrhineae, and a restricted distribution in the Mediterranean region, where generic diversity among Old World Antirrhineae is the greatest, *A. procumbens* evidently is more closely allied to taxa in the Old World. Even though its relationship among Old



World species in tribe Antirrhineae is obscure, it seems unnecessary and incorrect to look in the southwestern United States and Mexico for its relatives.

#### ACKNOWLEDGMENTS

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#### APPENDIX

Vouchered collections of 1) *Asarina procumbens* used in seed, pollen, and chromosomal studies, 2) *Neogaerrhinum* species whose chromosome numbers were determined, and 3) taxa used in the crossability studies. Voucher specimens are deposited at TEX-LL unless otherwise indicated.

#### Seed Coat Morphology and Anatomy.

*Asarina procumbens*. France: Dijon Bot. Gard., 1981; *Elisens* 613.

#### Pollen Morphology.

*Asarina procumbens*. Spain: Barcelona Bot. Gard., 1981; *Elisens* 799.

## Chromosome Number Determination.

*Asarina procumbens*,  $2n = 18$ . France: Dijon Bot. Gard., 1981; *Elisens* 613. Spain: Barcelona Bot. Gard., 1981; *Elisens* 799.

*Neogaerrhinum filipes*,  $2n = 30$ . United States: Nevada, *Elisens* 617.

## Crossability Studies.

*Asarina procumbens*. France: Dijon Bot. Gard., 1981; *Elisens* 613. Spain: Barcelona Bot. Gard., 1981; *Elisens* 799.

*Neogaerrhinum filipes*. United States: Nevada, *Elisens* 617.

*Maurandya*. *M. antirrhiniflora*. United States: Texas, Travis Co., *Elisens* 528. *M. barclatiana*. Mexico: Nuevo Leon, *Turner and Davies A-13*. *M. scandens*. Mexico: Oaxaca, *Elisens* 655. *M. wislizeni*. United States: Texas, Ward Co., *Elisens* 530.

*Mabrya*. *M. acerifolia*. United States: Arizona, Maricopa Co., *Elisens* 584. *M. erecta*. Mexico: Coahuila, *Gordon* 777. *M. geniculata*. Mexico: Sonora, *Gordon* 763.

*Lophospermum*. *L. atrosanguineum*. Mexico: Oaxaca, *Elisens* 665. *L. purpusii*. Mexico: Oaxaca, *Elisens* 549. *L. scandens*. Mexico: Morelos, *Elisens* 652.

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ANNOUNCEMENT

On Saturday, 28 September 1985, Huntington Botanical Gardens will host its Second Symposium on Succulent Plants. Featured will be the following speakers and their topics: A. Gibson, Univ. California, Los Angeles, The classification of cacti above the species level; M. Kimnach, Huntington Bot. Gard., The origins of epiphytic cacti; P. Nobel, Univ. California, Los Angeles, Environmental influences on agaves—Implications for establishment, tolerances, and productivity; C. Uhl, Cornell Univ., Polyploidy in *Echeveria* (Crassulaceae); G. Webster, Univ. California, Davis, Evolution and systematics of neotropical *Jatropha* and *Cnidoscolus* (Euphorbiaceae); A. Zimmerman, Univ. Texas, Systematics of the genus *Coryphantha* (Cactaceae).

Included in the day's events will be special tours of the recently opened Desert Garden Conservatory, an auction of rare plants, an optional luncheon and dinner, and an evening panel discussion. For information concerning registration and the schedule of events, please write: Succulent Plant Symposium, Huntington Botanical Gardens, 1151 Oxford Road, San Marino, CA 91108.